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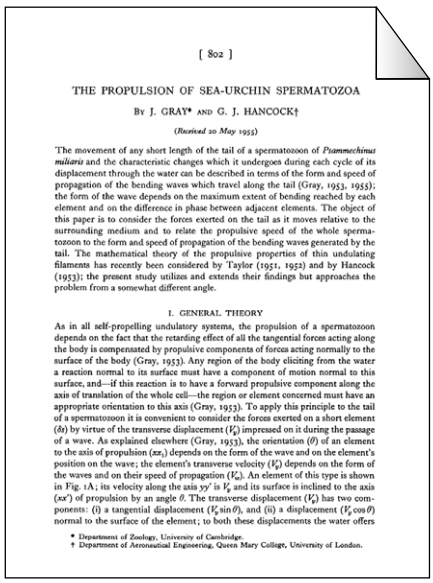
FLAGELLAR PROPULSION



[802]

THE PROPULSION OF SEA-URCHIN SPERMATOZOA

By J. GRAY* and G. J. HANCOCK†

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The movement of any short length of the tail of a spermatozoon of *Psammechinus miliaris* and the characteristic changes which it undergoes during each cycle of its displacement through the water can be described in terms of the form and speed of propagation of the bending waves which travel along the tail (Gray, 1953, 1955); the form of the wave depends on the maximum extent of bending reached by each element and on the difference in phase between adjacent elements. The object of this paper is to consider the forces exerted on the tail as it moves relative to the surrounding medium and to relate the propulsive speed of the whole spermatozoon to the form and speed of propagation of the bending waves generated by the tail. The mathematical theory of the propulsive properties of thin undulating filaments has recently been considered by Taylor (1951, 1952) and by Hancock (1953); the present study utilizes and extends their findings but approaches the problem from a somewhat different angle.

1. GENERAL THEORY

As in all self-propelling undulatory systems, the propulsion of a spermatozoon depends on the fact that the retarding effect of all the tangential forces acting along the body is compensated by propulsive components of forces acting normally to the surface of the body (Gray, 1953). Any region of the body eliciting from the water a reaction normal to its surface must have a component of motion normal to this surface, and—if this reaction is to have a forward propulsive component along the axis of translation of the whole cell—the region or element concerned must have an appropriate orientation to this axis (Gray, 1953). To apply this principle to the tail of a spermatozoon it is convenient to consider the forces exerted on a short element (δs) by virtue of the transverse displacement (V_y) impressed on it during the passage of a wave. As explained elsewhere (Gray, 1953), the orientation (θ) of an element to the axis of propulsion (sx_1) depends on the form of the wave and on the element's position on the wave; the element's transverse velocity (V_y) depends on the form of the waves and on their speed of propagation (V_w). An element of this type is shown in Fig. 1A; its velocity along the axis yy' is V_y and its surface is inclined to the axis (sx') of propulsion by an angle θ. The transverse displacement (V_y) has two components: (i) a tangential displacement ($V_y \sin\theta$), and (ii) a displacement ($V_y \cos\theta$) normal to the surface of the element; to both these displacements the water offers

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Charles J. Brokaw writes about Sir James Gray and G. J. Hancock's 1955 publication on the propulsion of sea urchin spermatozoa. Gray and Hancock's paper can be accessed free at the JEB archive.

In this JEB Classics paper, Sir James Gray and G. J. Hancock explained how spermatozoa are propelled by flagellar bending waves (Gray and Hancock, 1955). This paper was a lasting success because it provided an easy-to-understand solution to a complicated hydrodynamic problem, and because it provided a quantitative prediction of the swimming speed that was almost identical to the swimming speed measured in Gray's accompanying paper on the movement of sea urchin spermatozoa (Gray, 1955).

Gray came to this work with a full understanding of undulatory propulsion in long, thin animals such as snakes (Gray, 1953). Bending waves passing along the length of an elongated body will propel an animal forward if the body pushes laterally against its surroundings with a force that is greater than the force required to drag the body parallel to its length (see Fig. 1). But the microscopic realm, where momentum is insignificant, and the resistances are purely viscous, was uncharted territory. It was known that the viscous resistance of a very long thin body moving perpendicular to its length was twice the resistance moving parallel to its length (e.g. Burgers, 1938), but it was not known whether this fact had any relevance to an actively bending flagellum. Sir Geoffrey Taylor was the first to prove that propagated bending waves on a body in a viscous fluid would propel the body (Taylor, 1951; Taylor, 1952). Taylor's analysis was limited to very small amplitude waves, and could not be applied quantitatively to real situations, such as the sea urchin sperm flagellum, where the peak-to-peak amplitude is about one third of the wavelength. Hancock followed up on this by performing the difficult mathematical analysis required for sinusoidal bending waves with realistic amplitudes (Hancock, 1953). By discarding terms containing the value of the radius of the flagellum, he obtained an equation for the forward swimming velocity as a function of the frequency, amplitude and wavelength of the bending waves at the theoretical limit of 0 radius. Although it seems counterintuitive that a flagellum with 0 radius can propel a cell, this is a natural result of the 'no slip condition' for hydrodynamics in a viscous fluid, which requires that the velocity of fluid at the surface of a moving object must be the same as the velocity of the object. Hancock then used numerical calculations to explore the amount of reduction in velocity that occurred when the radius was greater than 0. From his analysis Hancock could see that, at least for a very thin filament, it was reasonable to estimate the forces on each small element along the length by treating each element as part of a straight filament moving at velocity V. By considering the filament in this way it was possible to multiply the local normal and longitudinal velocity components, V_N and V_L, by resistance constants, C_N and C_L, to calculate the force generated by each element (see Fig. 1). Gray and Hancock used this approximate method, now known as resistive force theory, to add up the

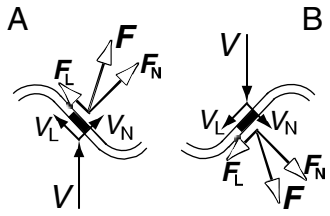

Fig. 1. A portion of a sperm flagellum that is propagating a bending wave, shown at two points in time in A and B. If the bending wave is moving from left to right, a short segment (dark bar) will be moving up in A and down in B, changing its tilt as the velocity changes. The velocity, V, of any segment can be resolved into a longitudinal component, V_L, and a normal component, V_N. Resistive force theory states that the force components pushing on the fluid will then be $F_L=C_L V_L$ and $F_N=C_N V_N$, where C_L and C_N are resistance constants. If $C_N>C_L$, the total force $F=F_N+F_L$ will always have a component pushing on the fluid in the direction of wave propagation, and this will provide a thrust in the opposite direction, propelling the spermatozoon to the left.

forces on each element resulting from bend propagation along the flagellum and from forward movement at an unknown velocity. The summation of all of these forces along the *x* axis must be 0, so the equation can be solved to obtain the forward propulsion velocity. It turns out that the resistance constants enter the forward velocity equation only as the ratio C_N/C_L, which is 2.0 for an infinitesimally thin filament. Gray's photographs of sea urchin spermatozoa revealed a waveform that could be approximated by a sine wave, so it was possible to use a sine wave as a model and integrate along the length. The use of resistive force theory was validated by the result that it generated the same equation for swimming velocity obtained from the more rigorous analysis in Hancock's 1953 paper. After adding the effect of the sperm head to the equations, the predicted velocity was almost exactly the same as Gray's measured velocity.

In effect, Gray and Hancock separated the analysis of movement in viscous fluids into two parts. One part, the calculation of the effects of radius and wavelength on the values of the resistance constants, remained the province of hydrodynamicists, who have reexamined the problem repeatedly. Much of this work is reviewed by Lighthill (Lighthill, 1976) and Dresdner et al. (Dresdner et al., 1980). The durability of the original conclusions results from the fact that the swimming velocity depends only on the ratio of the resistance constants, and hydrodynamic refinement usually changes C_N and C_L in the same direction, with minimal change in their ratio. The second part of the analysis, the use of resistance constants to analyze a particular movement pattern, was made accessible for biologists by Gray and Hancock's publication. Holwill and Burge used resistive force theory to analyze the swimming of bacteria with helical flagella (Holwill and Burge, 1963). I used it together with new descriptions of sperm flagellar bending waves as functions of length along the curve of the flagellum, rather than along a hypothetical *x* axis, to obtain simpler equations for calculating sperm swimming speed and energy expenditure (Brokaw, 1965; Brokaw, 1975). Actually, Carlson first used resistive force theory to calculate the energy expended against viscous resistances by a swimming sperm cell, by integrating the product of force and velocity along the length of the flagellum (Carlson, 1959). However, energy expenditure calculation requires absolute values of C_L, not just the ratio C_N/C_L. The value of C_L originally proposed by Hancock has been updated (Lighthill, 1976; Dresdner et al., 1980) leading to energy expenditures 35% greater than the first calculations. These new values still show that the energy output is well within the energy available from sperm metabolism. Resistive force theory is only a first order approximation to a very complex hydrodynamic problem. It is limited to specific cases where the fluid movement near any element along the length is perturbed in only a limited manner by the movement of nearby elements, and is not perturbed by any other influences, such as the presence and/or movement of other nearby objects in the fluid. More recent hydrodynamic work has attempted to develop methods for these situations, where simple resistive force theory cannot be used. For instance, it is inadequate for situations where a small flagellum is propelling a large cell, or where multiple, closely spaced flagella or cilia are producing movement. A new methodology developed to deal with such problems has succeeded in demonstrating that metachronal coordination of ciliary beating can be explained by hydrodynamic interactions between cilia (Gueron and Levit-Gurevich, 2001).

Resistive force theory, like the Stokes equations on which it is based, is a linear theory, which makes it easily invertible to calculate velocities resulting from specified forces. This, in fact, is exactly what Gray and Hancock did, to calculate the forward swimming velocity. More recently, resistive force theory has been used for simulations of flagellar movement, which use ideas about internal force generation to calculate the form and propagation of flagellar bending waves as well as velocities of movement in a viscous environment. These simulations require computations of rates of flagellar bending at many points along a flagellum, given a specified distribution of internal active forces. The result is a set of equations with many unknown velocities, which can be solved by standard numerical methods as long as the velocities are linear functions of all of the force specifications (Brokaw, 1972; Hines and Blum, 1978; Brokaw, 2002; etc.). Since the mechanisms actually used by flagella to initiate and propagate bending waves are still unknown, resistive force theory is still being actively used for these investigations, and more than 20% of the citations of this 1955 JEB Classics paper have accumulated since January 2000. These include new and unexpected interest from the field of nanotechnology, seeking to construct microscopic artificial swimmers that mimic the movements of spermatozoa (e.g. Dreyfus et al., 2005).

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